

# First record of the parasitoid subfamily Doryctinae (Hymenoptera, Braconidae) in Rovno amber: description of a new genus and species with stigma-like enlargement on the hind wing of the male

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## Abstract

A new genus and species of the braconid parasitoid subfamily Doryctinae, *Eocenhecabolus kotenkoi* **gen. et sp. nov.**, from the late Eocene Rovno amber are described and illustrated. *Eocenhecabolus* **gen. nov.** is the first unambiguously extinct Doryctinae genus. This genus is described from the male and characterised by the followings features: in the fore wing by the postfurcal position of the recurrent vein (m-cu) relatively to the first radiomedial vein (2-SR), and a distally open brachial (second subdiscal) cell; in the hind wing by the presence of the elementary stigma-like enlargement on the distal half of the costal (1-SC+R) vein. The different types of stigma-like enlargements found in the hind wings of males in the subfamily Doryctinae are discussed.

## Keywords

Coleoptera, description, Eocene, fossil, Hecabolini, *Hemidoryctes*, stigma-like enlargement

## Introduction

The subfamily Doryctinae is morphologically one of the most diverse groups of idiobiont parasitoids of the family Braconidae (Zaldivar-Riverón et al. 2008; Quicke 2015). For development, they predominantly use the larval stages of the hosts from the order Coleoptera and rarely Lepidoptera, Hymenoptera and perhaps Isoptera; however, a few tropical (especially Neotropical) taxa are known as phytophages (gall-associated – inquiline or inducer) (Zaldivar-Riverón et al. 2008, 2014; Belokobylskij and Maetô 2009; Yu et al. 2016).

The unambiguous doryctine fossil taxa mainly have been described or recorded as inclusions in fossil resin (Taimyr retinite, Baltic, Mexican and Dominican ambers) (Brues 1933; Muesebeck 1960; Zherikhin 1978; Zuparko and Poinar 1997), and only a few are known from rock fossils (Statz 1936, 1938; Belokobylskij 2014). The most common fossil doryctine genus is *Doryctes* Haliday, 1836 (~ 14 species), although some species may belong to *Ontsira* Cameron, 1900 because sometimes it is very difficult to separate the fossil representatives of these genera (Brues 1933; Statz 1938; Belokobylskij 2014). One species of the genus *Rhaconotus* Ruthe, 1954 (described as *Ichneumon petrinus* Scudder, 1877 (Scudder 1890) and later (Brues 1910) transferred to *Hormiopterus* Giraud, 1869) was recorded from a rock fossil of the Florissant Lagerstätte (latest Eocene), but this determination is doubtful given the short and character's reduced description and incomplete illustrations. Additionally, three late Oligocene species of the genus *Spathius* Nees, 1818 have been described by Statz (1936, 1938) from rock fossils of Rott Lagerstätte, but its descriptions are ambiguous and they could be representatives of other doryctine genera or even non-doryctines.

Four reported extant genera with described fossil species belong to the doryctine tribe Hecabolini, but the taxonomic positions of all these records are questionable. The morphological characters of *Hecabolus gladiator* Statz, 1936 (rock fossil from Rott) indicate that it is likely a member of the brachistine genus *Eubazus* Nees, 1814. The extinct *Promonolexis klebsi* Brues, 1933 (Baltic amber) is probably a synonym of the brachistine genus *Blacus* Nees, 1818 (Belokobylskij 2014). The fossil *Polystenus obduratus* Brues, 1933 (Baltic amber) is actually not a representative of the genus *Polystenus* Foerster, 1862 and perhaps not Doryctinae, but its status is difficult to justify based on the description and requires re-examination of the type (which is perhaps lost) or additional specimens. According to the description, the extinct *Semirhytus caudatus* Brues, 1933 (Baltic amber) is probably a member of the subfamily Rogadinae rather than Doryctinae. Additionally, there is a very doubtful record of the specialised doryctine genus *Heterospilus* Haliday, 1836 from the Late Cretaceous (Santonian) Taimyr amber (Zherikhin 1978) and this hypothesis requires verification.

The real taxonomic position of the fossil species *Doryctomorpha tertiaria* Brues, 1933 (Baltic amber), described originally in the New Zealand endemic genus *Doryctomorpha* Ashmead, 1900 (currently considered to be within the subfamily Mesostoinae: Quicke et al. 2020; Jasso-Martinez et al. 2022) remains unclear. Unfortunately, the original description and illustration (Brues 1933) are insufficient for an accurately taxonomic placement of this species, so the type must be found and verified or new material made available for certainty.

Unlike the fossil doryctine braconids listed above, the systematic position of two other taxa belonging to the tribe Ecphylini is beyond doubt. The discovery of two specialised doryctine genera *Ecphyllus* Foerster, 1862 with *E. oculatus* Muesebeck, 1960, and *Aivalykus* Nixon, 1938 with *A. dominicanus* Zuparko & Poinar, 1997 in Miocene Mexican and Dominican ambers is interesting and valuable (Muesebeck 1960; Zuparko and Poinar 1997). The extant members of both these genera are known as parasitoids of predominantly bark beetles (Curculionidae, Scolytinae) larvae.

Rovno amber is coeval with late Eocene Baltic amber, which has yielded more than 310 new arthropod species, and nearly all are unknown from Baltic amber (Makarkin et al. 2022). Recently, Varash District localities have yielded dozens of taxa unknown from the better studied Klesov deposit (Telnov et al. 2022; Dietrich et al. 2023), many of which were found in Velyki Telkovichi (e.g. Simutnik et al. 2020; Legalov et al. 2022a).

Only two recently published records exist for Rovno amber braconids: description of a new species of *Microtypus* Ratzeburg, 1848 (Belokobylskij et al. 2021), and report about the presence of the aphidiine genus *Toxares* Haliday, 1840 (Kalyuzhna and Perkovsky 2021).

This paper provides an illustrated description of the male of a new doryctine genus and species discovered in late Eocene Rovno amber which is characterized by the presence of a stigma-like enlargement on the hind wing and an open distally brachial (first subdiscal) cell of the fore wing.

## Materials and methods

A well preserved, mainly complete parasitoid was found in the clear piece VT-729 (36 × 27 × 17 mm, weight 7 grams before primary treatment) of the collection from Velyki Telkovichi, Varash District, Rovno Oblast.

The specimen was examined using the equipment and techniques described in Simutnik et al. (2022a). Photographs were taken using a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with LAS Core. The final plates were prepared in Adobe Photoshop CS6.

The terminology employed for morphological features and sculpture, as well as body measurements follow Belokobylskij and Maetô (2009). Wing venation nomenclature also follows Belokobylskij and Maetô (2009), with the terminology of van Achterberg (1993) shown in parentheses.

The specimen used for this study is deposited in the collection of the I.I. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (**SIZK**).

## Systematic part

**Class Insecta Linnaeus, 1758**

**Order Hymenoptera Linnaeus, 1758**

**Family Braconidae Nees, 1811**

**Subfamily Doryctinae Foerster, 1863**

**Genus *Eocenhecabolus* Belokobylskij, gen. nov.**

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**Type species.** *Eocenhecabolus kotenkoi* Belokobylskij, gen. et sp. nov., by present designation and monotypy.

**Etymology.** Named after “Eocene” from the geological epoch dated to the Rovno amber and the generic name of its extant type genus *Hecabolus* of the tribe Hecabolini from subfamily Doryctinae. Gender: masculine.

**Description.** *Head* (Fig. 1E, F, H) not depressed, weakly transverse. Ocelli medium-sized, weakly convex, arranged in triangle with base 1.3 times its sides. Frons almost not convex, without lateral protuberances. Eyes large, oval, glabrous. Face distinctly convex. Malar suture present, but weak. Clypeus relatively high, with distinct lower visor. Clypeal suture fine laterally, absent on wide distance dorsally. Anterior tentorial pits small. Occipital carina present and distinct at least laterally and dorsally. Mandibles robust. Maxillary palpus medial length. *Antenna* (Fig. 1C, E, H) mostly missing, only four segments present. Scape short and wide, approximately as long as maximum width. Pedicel relatively short and thick, about as long as scape. First flagellomere long, subcylindrical, weakly curved and without any modifications. *Mesosoma* (Fig. 1C, G) not depressed. Pronotum convex in posterior half, with distinct short longitudinal lateral carinae. Sides of pronotum mainly smooth with short rugae on oblique furrow. Mesoscutum distinctly (but not highly) roundly convex above pronotum, densely and rather distinctly granulate-punctate. Notauli present, deep and complete, reaching prescutellar furrow. Scutellum convex. Prepectal carina present, distinct. Mesopleuron mainly smooth. Precoxal sulcus present, but short (not more than half of mesopleuron length below), rather deep, almost straight, finely crenulate. Metascutum without dorsal tooth (lateral view). Propodeum evenly curved in lateral view, with areas delineated but distinct carinae, with wide, sub-round and smooth basolateral areas, with narrow and long areola, distinctly separated petiolate area and relatively short basomedial carina; without lateral tubercles; propodeal spiracle sub-circular. *Wings* (Figs 1A, B, 2A). Fore wing relatively wide, evenly faintly infusate; pterostigma rather long and wide. Radial (marginal) cell not shortened, closed distally, wide, about 3.5 times longer than its maximum width. Metacarp (1-R1) 1.2 times longer than pterostigma. Radial vein (r) arising weakly before middle of pterostigma. First medial abscissa (1-SR+M) present and weakly sinuate. Both radiomedial veins (2-SR and r-m) present. Second radiomedial (submarginal) cell relatively long, pentagonal. Discoidal (first discal) cell petiolate anteriorly; petiole (1-SR) short. Recurrent vein (m-cu) distinctly postfurcal, weakly convergent posteriorly with basal vein (1-M). First mediocubital vein (M+CU1) well sclerotised and straight. Nervulus (cu-a) distinctly postfurcal. Brachial (first subdiscal) cell open posteriorly; brachial vein (CU1b) absent. Transverse anal veins (2A and a) absent. Hind wing. Second abscissa of costal vein (1-SC+R) with elementary elliptic stigma-like enlargement. Radial vein (SR) unsclerotised and transparent. Nervellus (cu-a) present. Submedial (subbasal) cell large. First abscissa of mediocubital vein (M+CU) more than twice longer than second abscissa



(1-M). **Legs** (Figs 1C, D, 2B) rather robust and short. Fore tibia with distinct spines arranged almost in single line. Hind coxa elongate, without ventro-basal tubercle and corner, weakly shorter than propodeum. Hind femur short and wide, 0.7 times as long as hind tibia. Hind tibia weakly thickened distally, with at least two distinctly visible spines on its dorsal margin in distal quarter. Hind tibial spur glabrous, relatively short, about 0.3 times as long as hind basitarsus. Hind basitarsus short, about half as long as second to fifth segments combined. Tarsal claw medium size, simple and evenly curved. **Metasoma** (Figs 1C, D, G, 2B) elongate, oval in dissection, not pressed, segments behind third one distinctly exposed posteriorly. First metasomal tergite not wide, weakly widened distally, with deep dorsope, with distinct dorsomedial carinae situated closed to each other, with distinct lateral carinae, striate medially and smooth laterally, with spiracles situated on basal third of tergite, spiracular tubercles small, weakly shorter than second and third tergites combined. Suture between second and third tergites absent. Second tergite mainly smooth, with shallow and short sublateral depression. Laterotergites (epipleura) of segments behind first one perhaps not separated; spiracles placed on the lateral part of tergites. Genitalia distinctly visible from below.

**Comparative diagnosis.** This new genus belongs to the tribe Hecabolini based on the fore wing with a distally open brachial (subdiscal) cell and the hind wing of male with an elementary stigma-like enlargement. The latter character is similar to that found in the extant doryctine genera *Hemidoryctes* Belokobylskij, 1992, *Dendrosoter* Wesmael, 1838, *Bracocesa* Koçak & Kemal, 2008, and *Doryctophasmus* Enderlein, 1912.

*Eocenhecabolus* gen. nov. is most similar to the Pantropical *Hemidoryctes* Belokobylskij from the subtribe Stenocorsina (Doryctinae: Hecabolini) by the wing venation and analogous enlargement on the hind wing. However, the new genus differs from *Hemidoryctes* by the very short antennal scape, approximately as long as its maximum width (elongated, about 1.5 times longer than the maximum width of that in *Hemidoryctes*), the enlarged pedicel, about as long as the scape (not enlarged and only about 0.5 times as long as the scape in *Hemidoryctes*), the mostly smooth temple with additional sparse punctuation (densely granulate-striate in *Hemidoryctes*), the mostly smooth side of the mesosoma (basically densely granulate in *Hemidoryctes*), the propodeum with areas delineated by distinct carinae (without areas delineated by carinae in *Hemidoryctes*), the fore wing not maculate, but only faintly infusate (distinctly maculate in *Hemidoryctes*), the distinctly postfurcal recurrent vein (m-cu) of the fore wing (usually distinctly antefurcal in *Hemidoryctes*), the relatively short discoidal (discal) cell of the fore wing (distinctly elongate in *Hemidoryctes*), the weakly postfurcal nervulus (cu-a) in the fore wing (strongly postfurcal in *Hemidoryctes*), the first abscissa of the mediocubital vein (M+CU) of the hind wing distinctly longer than the second abscissa (1-M) (distinctly shorter in *Hemidoryctes*), the smooth and less thick hind femur, 3.0 times longer than its maximum width (densely granulate-reticulate and thicker, 2.5 times longer in *Hemidoryctes*), the hind tibia with relatively long setae and at least two distinct spines on its dorsal margin (with very short setae and without spines on the dorsal margin in *Hemidoryctes*), the shortened hind tarsus with the segment not narrowed toward its distal margin (elongate and segments distinctly narrowed distally in

*Hemidoryctes*), and the smooth metasoma behind the first tergite (the second and part of third tergites heavily sculptured in *Hemidoryctes*).

Apart from several individual differences, the new genus differs from other three extant genera exhibiting stigma like enlargement on hind wing (*Dendrosoter* Wesmael, *Bracocesa* Koçak & Kemal and *Doryctophasmus* Enderlein) in having the open distally brachial (first subdiscal) cell and no brachial vein (CU1b) in the fore wing (this cell closed distally and the brachial vein present in all latter genera), and large submedial (subbasal) cell in the hind wing with the first abscissa of the mediocubital vein (M+CU) distinctly longer than the second abscissa (1-M) (this cell small and the first abscissa short in all three latter genera).

Among known fossil Doryctinae genera, *Eocenhecabolus* gen. nov. is superficially similar to the extinct *Doryctomorpha tertiaria* Brues, 1933 described based on a female from Baltic amber (Brues, 1933). However, the assignment of this species to the peculiar endemic New Zealand genus *Doryctomorpha* Ashmead, 1900 from the subfamily Mesostoinae is very doubtful and unsupported by known morphological characters. The female of *D. tertiaria* Brues perhaps may belong to the new genus described here, but absence of important information in this species description (especially regarding wing venation and legs) and uninformative figure together with the loss of the type specimen prevent us to form a reliable opinion about its placement. Anyway, *Eocenhecabolus kotenkoi* gen. et sp. nov. differs from *D. tertiaria* Brues by having the head transverse in dorsal view, with a transverse diameter of eye 1.5 times longer than the temple (head subquadrate and with a transverse diameter of eye 2.0 times longer than the temple in *D. tertiaria*), the vertex transversely and sinuately striate (smooth in *D. tertiaria*), the propodeum with areas distinctly delineated by carinae (without areolation in *D. tertiaria*), and the hind coxa suboval and without a prominent lower corner (subtriangular and with a prominent lower corner in *D. tertiaria*).

***Eocenhecabolus kotenkoi* Belokobylskij, sp. nov.**

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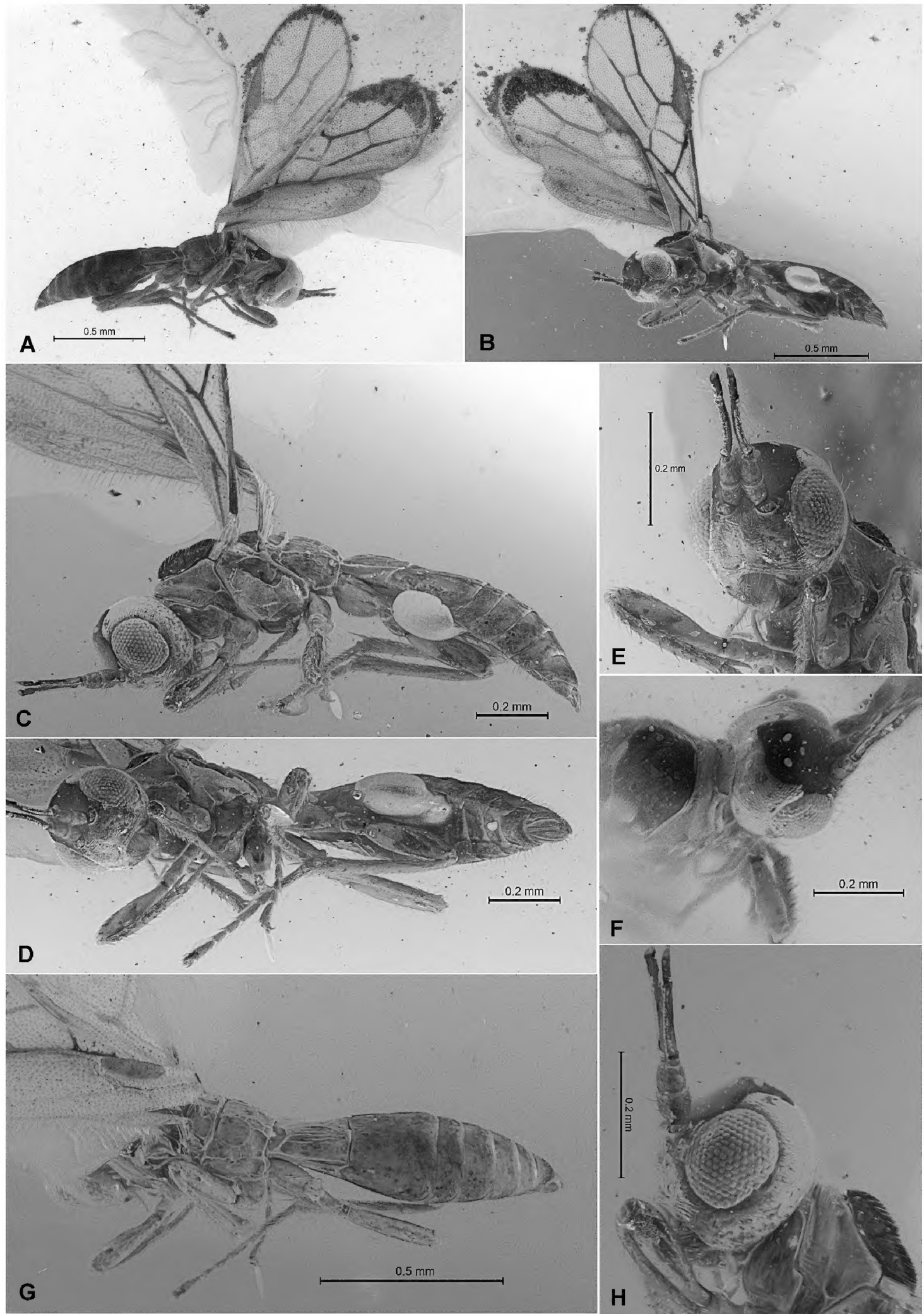
Figs 1, 2

**Type material. Holotype:** male, SIZK VT-607, Velyki Telkovichi, Varash District, Rovno amber, late Eocene.

**Description. Male.** Body length 1.5 mm; fore wing length 1.3 mm.

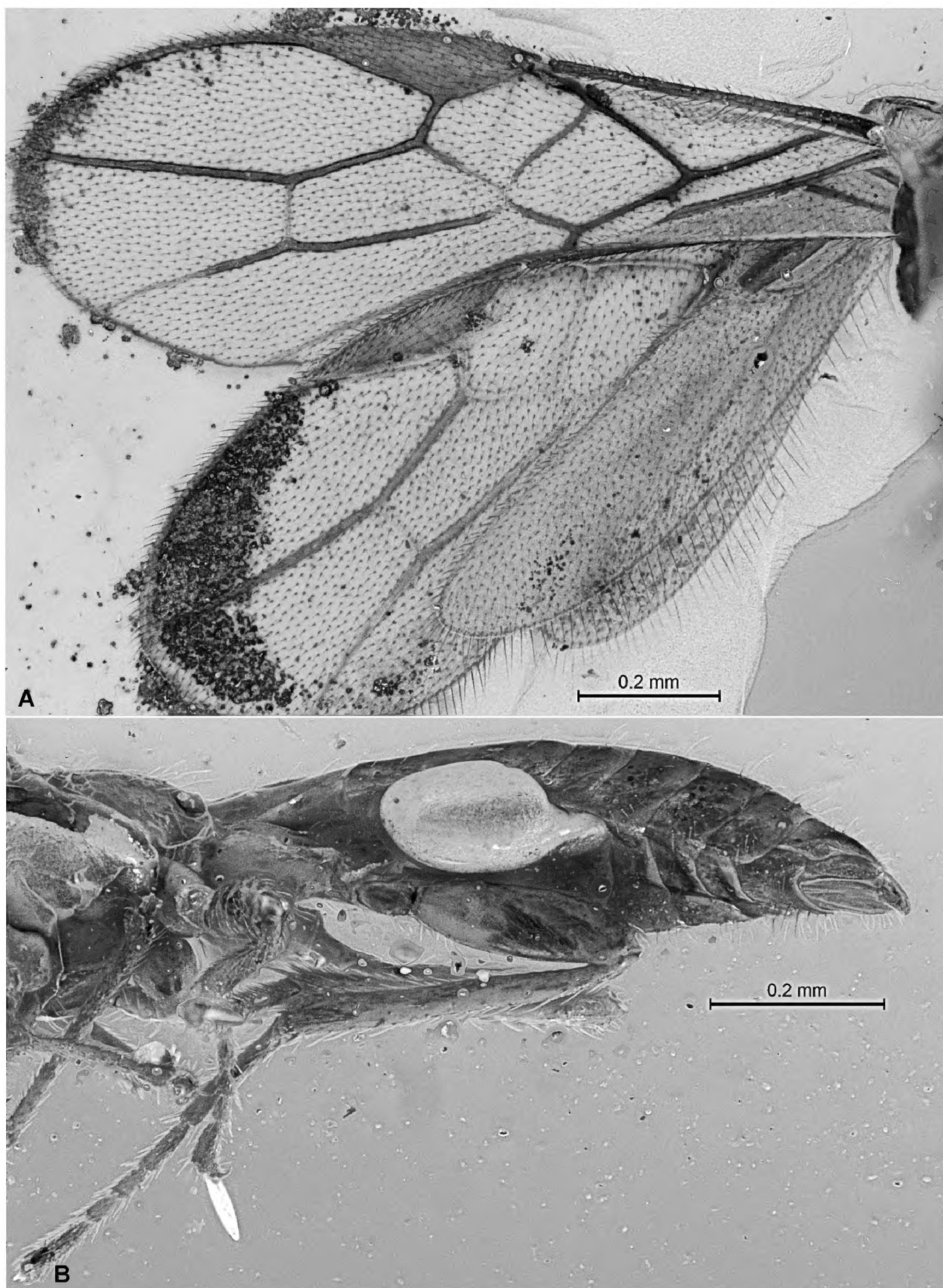
**Head:** Head relatively high, its width about 1.3 times medial length. Occiput weakly concave. Transverse diameter of eye 1.5 times longer than temple (subdorsal view). POL 1.3 times Od, approximately 0.5 times OOL. Eye about 1.2 times as high as broad (lateral view). Malar space 0.3 times height of eye, almost equal to basal width of mandible. Face width 0.9 times height of eye, 1.3 times medial height of face and clypeus combined. Hypoclypeal depression subround, its transverse width 0.9 times distance from edge of depression to eye, 0.4 times width of face.

**Antenna:** First flagellomere almost 7.0 times longer than its apical width, approximately twice longer than scape. Second segment present only basally, remaining part missing.



**Figure 1.** *Eocenhecabolus kotenkoi* gen. et sp. nov. (male, holotype, Rovno amber, # SIZK VT-607) **A** habitus, right dorso-lateral view **B** habitus, left ventro-lateral view **C** body, lateral view **D** body, ventro-lateral view **E** head and antenna, fronto-lateral view **F** head, dorsal view **G** propodeum and metasoma, dorsal view **H** head and antenna, lateral view.





**Figure 2.** *Eocenhecabolus kotenkoi* gen. et sp. nov. (male, holotype, Rovno amber, # SIZK VT-607)  
**A** wings **B** metasoma and hind leg, lateral view.

**Mesosoma:** Mesosoma long, its length 1.8 times height. Neck of prothorax relatively short. Pronotal carina absent, dorsal pronotal lobe distinctly convex. Median lobe of mesoscutum convex, distinctly protruding forward, without anterolateral



corners. Prescutellar depression relatively long. Subalar depression shallow and mainly smooth. Lateral carinae between propodeum and metapleuron strong and complete.

**Wings:** Fore wing wide, 2.6 times longer than its maximum width. Pterostigma wedge-shaped, 3.7 times longer than its width. Radial vein (r) arising from basal 0.4 of pterostigma. First (r) and second (3RSa) radial abscissae forming obtuse angle; first abscissa (r) 0.7 times as long as maximum width of pterostigma. Second radial abscissa (3RSa) 3.0 times first abscissa (r), 0.5 times as long as the straight third abscissa (3RSb), 1.3 times longer than the straight first radiomedial vein (2RS). Second radiomedial (submarginal) cell relatively wide and long, 2.7 times longer than its maximum width, 1.8 times longer than the narrow brachial (first subdiscal) cell. Recurrent vein (1 m-cu) 0.75 times as long as first radiomedial vein (2RS), 0.6 times as long as basal vein (1M). Discoidal (first discal) cell rather short, 1.7 times longer than its maximum width. Nervulus (1cu-a) 0.6 times as long as distance between basal (1M) vein and nervulus (1cu-a). Parallel vein (2CUB) weakly curved basally. Brachial (second subdiscal) cell relatively short and narrow. Hind wing almost 4.5 times longer than its maximum width. Stigma-like enlargement 3.5 times longer than maximum width. First abscissa of mediocubital vein (M+CU) almost twice longer than second abscissa (1-M).

**Legs:** Fore femur about 4.5 times longer than maximum width. Fore tarsus 1.2 times longer than fore tibia. Hind coxa almost 1.5 times longer than its maximum width, 0.8 times as long as propodeum. Hind femur 3.0 times longer than its width. Hind tarsus almost as long as hind tibia. Second segment of hind tarsus 0.4 times as long as basitarsus, weakly longer than fifth segment (without pretarsus).

**Metasoma:** Length 1.2 times larger than length of head and mesosoma combined. First metasomal tergite 1.4 times longer than distal maximum width, 1.3 times longer than propodeum; apical width of first tergite about 1.6 times its basal width. Second and third tergites combined 1.3 times longer than basal width of second tergite, 0.9 times as long as their maximum width.

**Sculpture and pubescence:** Temple densely transversely and sinuately striate with additional reticulation laterally. Face weakly transversely striate, smooth medially. Frons and most part of temple perhaps mainly smooth. Propodeum mostly smooth, only sometimes with short and sparse rugae along carinae; areola almost 2.5 times longer than its width; basomedial carina present in basal 0.3 of propodeum. Hind coxa and femur smooth. First metasomal tergite striate medially, weakly rugose sublaterally, almost smooth laterally. Second tergite mainly smooth, finely striate in small basolateral areas. Remaining part of metasoma smooth. Hind tibia with rather dense and short semi-erect setae, its length 0.4–0.6 times maximum width of tibia.

**Colour:** Body almost entirely brown. Legs mainly reddish brown to pale reddish brown. Fore wing almost entirely faintly evenly infusate. Pterostigma entirely brown.

**Female.** Unknown.

**Etymology.** This species is named in honour of the well-known Ukrainian brconidologist, Dr Anatoly Grigorievich Kotenko.

## Discussion

The fossil braconid taxa from the subfamily Doryctinae are relatively common in the Paleogene and Neogene compared to the members of many other braconid subfamilies. Most of these taxa have been attributed to extant genera (*Doryctes* Haliday, *Ontsira* Cameron, *Rhaconotus* Ruthe, *Spathius* Nees, *Polystenus* Foerster, *Ecphylus* Foerster, *Aivalykus* Nixon, *Hecabolus* Wesmael, *Semirhytus* Szépligeti and *Heterospilus* Haliday). Only one genus known from a fossil, monotypic *Promonolexis* Brues, 1933 from Baltic amber (the type species *P. klebsi* Brues, 1933), was described in Doryctinae (Brues 1933), but actually it may belong to the genus *Blacus* Nees (Brachistinae) (Belokobylskij 2014). *Eocenhecabolus* gen. nov. is the first unambiguously extinct genus of Doryctinae.

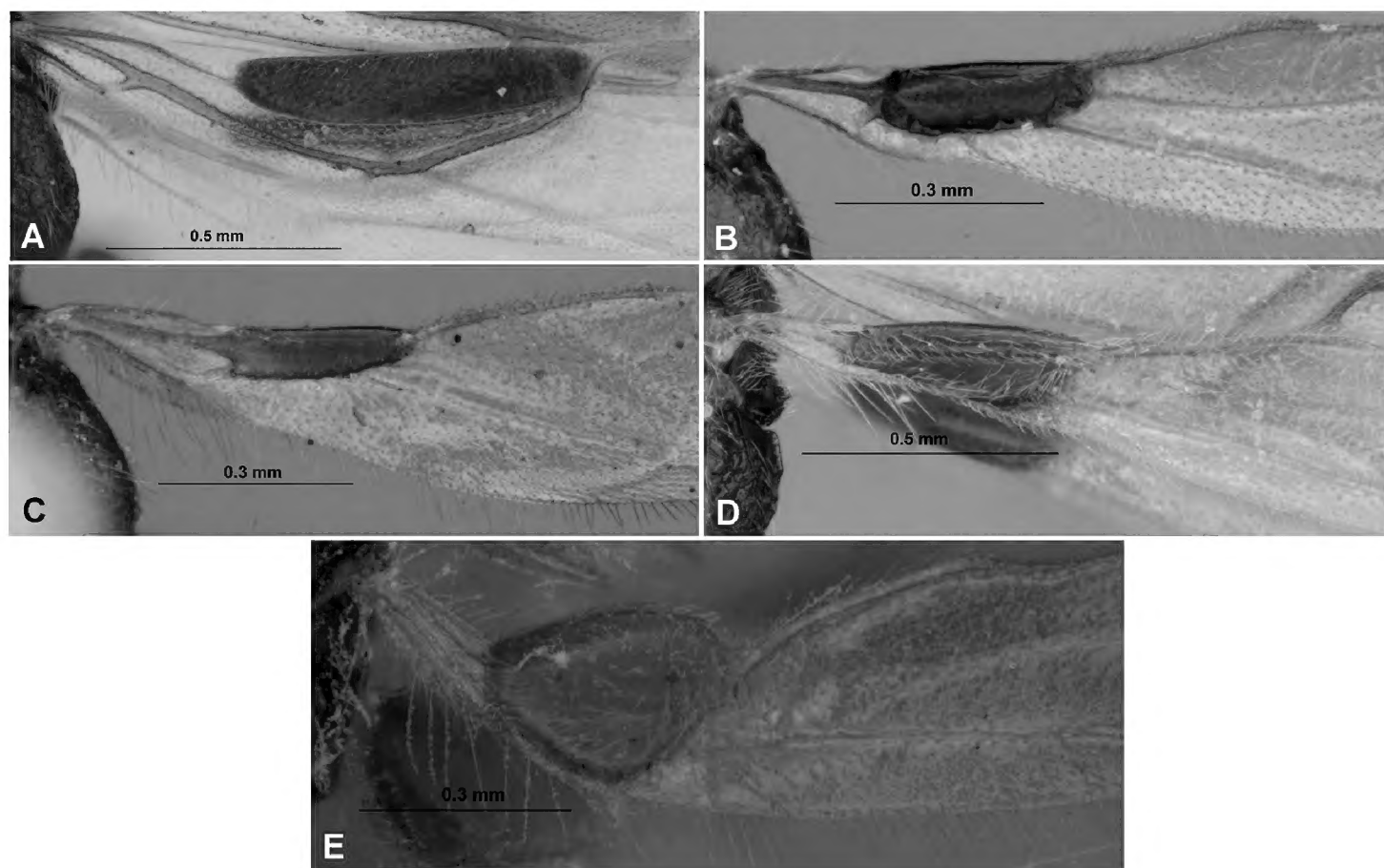
*Eocenhecabolus* gen. nov. is the first recorded extinct doryctine representative with a stigma-like enlargement on the hind wing. Similar structures on the hind wing are known in numerous males of extant genera, predominantly from the tribes Hecabolini and Heterospilini, but a few taxa with such enlargement of an elementary type also have been recorded in the tribe Doryctini. The functional role of this structure in males is not fully understood, but it may have sensory or sexual attraction functions.

According to the morphological investigation of this structure in extant Doryctinae (Belokobylskij 1983) three types of hind wing stigma-like enlargement in males are known (Fig. 3):

1. elementary, “*Dendrosoter*” type (Fig. 3A) – relatively flat widened distal part of the second costal vein (1-SC+R) with its ventral (and dorsal) surface entirely evenly covered by short setae; the hind wing usually with a recurrent vein (m-cu), and a nervulus (cu-a) arising from the mediocubital vein (M+CU) and not connected to the enlargement (*Dendrosoter*, *Bracocesa*, *Doryctophasmus*, *Hemidoryctes*).

2. moderately modified, “*Hecabolus*” type (Fig. 3B, C) – dorsally convex stigma-like enlargement of the hind wing connected not only to the costal vein (1-SC+R), but also to the mediocubital (M+CU) and basal (1r-m) veins; the enlargement weakly bent downward only anteriorly and its margin without eyelash-like setae; with setae on the ventral surface rather evenly distributed; the nervulus (cu-a) arising from the posterior margin of enlargement, and the recurrent vein (m-cu) often absent (many members of the tribe Hecabolini).

3. complex, “*Heterospilus*” type (Fig. 3D, E) – dorsally convex stigma-like enlargement of the hind wing connected to three veins of the hind wing (costal (1-SC+R), mediocubital (M+CU) and basal (1r-m)); most of its margins are bent downward (except places where the veins originate), especially anteriorly; the margins of the curved parts covered by eyelash-like setae; additionally present small and setose ear-shaped process inside of the lower (inner) surface of the enlargement; wide large area of the ventral surface of the enlargement glabrous; the nervulus (cu-a) arising from posterior margin of the enlargement, and the recurrent vein (m-cu) always absent (most members of the tribe Heterospilini).



**Figure 3.** Stigma-like enlargement on the male hind wing **A** *Dendrosoter middendorffii* (Ratzeburg, 1848) **B** *Leluthia hungarica* (Szépligeti, 1900) **C** *Leluthia transcaucasica* (Tobias, 1976) **D** *Heterospilus tauricus* Telenga, 1941 **E** *Heterospilus* sp.

The host of *Eocenhecabolus kotenkoi* gen. et sp. nov. is unknown. However, it perhaps belongs to the tribe Hecabolini, the members of which are predominantly known as ectoparasitoids of coleopteran larvae. Coleopteran larvae in Rovno amber are abundant (Perkovsky 2016; Haug et al. 2022), but largely understudied. Many of the better studied Rovno amber flat wasps (Bethylidae) as well as extant ones also are often known as beetle parasitoids, and nearly all Rovno bethylids (14 of 15) are unknown in the Baltic amber fauna (Colombo et al. 2021 and references therein) as are 85% of Rovno amber beetle species (Legalov et al. 2022b). Thus, it is assumed that the braconid ectoparasitoids of coleopteran larvae in Rovno amber could be mostly different from those in Baltic amber.

*Eocenhecabolus kotenkoi* gen. et sp. nov. is the 24<sup>th</sup> non-ant hymenopteran genus (from 58, 41.4%) and 51<sup>st</sup> non-ant hymenopteran species (from 74, 68.9%) found in Rovno amber but unknown from Baltic amber (Simutnik et al. 2022a, b).

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## References

- Belokobylskij SA (1983) To the knowledge of the genera *Heterospilus* Hal. and *Dendrosotinus* Tel. (Hymenoptera, Braconidae) of the USSR fauna. Proceedings of the All-Union Entomological Society 65: 168–186. [In Russian]
- Belokobylskij SA (2014) Family Braconidae. In: Antropov AV, Belokobylskij SA, Compton SG, Dlussky GM, Khalaim AI, Kolyada VA, Kozlov MA, Perfilieva KS, Rasnitsyn AP (Eds) The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK. Earth and Environmental Sciences Transactions of the Royal Society of Edinburgh 104(3–4): 335–446. <https://doi.org/10.1017/S1755691014000103>
- Belokobylskij SA, Maetô K (2009) Doryctinae (Hymenoptera, Braconidae) of Japan. Fauna mundi (Vol. 1). Warszawska Drukarnia Naukowa, Warszawa, 806 pp.
- Belokobylskij SA, Pankowski MG, Pankowski MV, Zaldívar-Riverón A (2021) A new genus and three new species of fossil braconid wasps (Hymenoptera, Ichneumonoidea) from Eocene Baltic and Rovno ambers. Journal of Paleontology 95(6): 1259–1272. <https://doi.org/10.1017/jpa.2021.47>
- Brues CT (1910) The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. Bulletin of the Museum of Comparative Zoology at Harvard University 54: 1–125.
- Brues CT (1933) The parasitic Hymenoptera of the Baltic amber. Bernstein Forschungen 3: 4–178.
- Colombo WD, Perkovsky EE, Vasilenko DV (2021) The first sclerodermine flat wasp (Hymenoptera: Bethyridae) from the upper Eocene Rovno amber, Ukraine. Alcheringa: An Australasian Journal of Palaeontology 45: 429–434. <https://doi.org/10.1080/03115518.2021.2006311>
- Dietrich CH, Simutnik SA, Perkovsky EE (2023) Typhlocybinae leafhoppers (Hemiptera: Cicadellidae) from Eocene Rovno amber reveal a transition in wing venation and a defensive adaptation. Journal of Paleontology. [in press]
- Haug C, Baranov VA, Hörnig MK, Gauweiler J, Hammel JU, Perkovsky EE, Haug JT (2022) 35 million-year-old solid-wood-borer beetle larvae support the idea of stressed Eocene amber forests. Palaeobiodiversity and Palaeoenvironments. <https://doi.org/10.1007/s12549-022-00552-0>
- Jasso-Martinez JM, Quicke DLJ, Belokobylskij SA, Santos BF, Fernandez-Triana JL, Kula RR, Zaldivar-Riveron A (2022) Mitochondrial phylogenomics and mitogenome organization in the parasitoid wasp family Braconidae (Hymenoptera: Ichneumonoidea). BMC Ecology and Evolution 22(46): 22–46. <https://doi.org/10.1186/s12862-022-01983-1>

- Kaliuzhna MO, Perkovsky EE (2021) A first possible record of fossil *Toxares* (Hymenoptera, Braconidae, Aphidiinae) from Rovno amber. International Society of Hymenopterists #Hymathon2021 virtual symposium 6–7 May 2021: 19–19. [https://www.hymenopterists.org/wp-content/uploads/2021/04/Hymathon2021\\_Program\\_.pdf](https://www.hymenopterists.org/wp-content/uploads/2021/04/Hymathon2021_Program_.pdf)
- Legalov AA, Nazarenko VY, Vasilenko DV, Perkovsky EE (2022a) *Ceutorhynchus* Germar (Coleoptera, Curculionidae) as proxy for Eocene Brassicaceae: first record of the genus from Rovno amber. Journal of Paleontology 96(2): 379–386. <https://doi.org/10.1017/jpa.2021.82>
- Legalov AA, Vasilenko DV, Perkovsky EE (2022b) The American tribes Anypotactini and Eudiagogini (Coleoptera, Curculionidae) in Eocene of Europe as indicators of Eocene climate with description a new species. Diversity 14(9): 767–767. <https://doi.org/10.3390/d14090767>
- Makarkin VN, Perkovsky EE, Anisyutkin LN, Dubovikoff DA (2022) First larvae of Raphidioptera from Eocene Sakhalinian and Rovno ambers. Zootaxa 5219(5): 456–466. <https://doi.org/10.11646/zootaxa.5219.5.4>
- Muesebeck CFW (1960) A fossil braconid wasp of the genus *Ecphylus* (Hymenoptera). Journal of Paleontology 34(3): 495–496.
- Perkovsky EE (2016) A new species of Micromalthidae (Coleoptera) from the Rovno amber: 1. Adult morphology. Paleontological Journal 50(3): 293–296. <https://doi.org/10.1134/S0031030116030047>
- Quicke DLJ (2015) The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics Evolution and Ecology. Wiley Blackwell, Chichester, 688 pp. <https://doi.org/10.1002/9781118907085>
- Quicke DLJ, Belokobylskij SA, Braet Y, van Achterberg C, Hebert PDN, Prosser SWJ, Austin AD, Fagan-Jeffries EP, Ward DE, Shaw MR, Butcher BA (2020) Phylogenetic reassignment of basal cyclostome braconid parasitoid wasps (Hymenoptera) with description of a new, enigmatic Afrotropical tribe with a highly anomalous 28S D2 secondary structure. Zoological Journal of the Linnean Society 190: 1002–1019. <https://doi.org/10.1093/zoolinnean/zlaa037>
- Scudder SH (1890) The Tertiary insects of North America. Report of the United States Geological Survey of the Territories 13: 1–734. <https://doi.org/10.5962/bhl.title.2507>
- Simutnik SA, Perkovsky EE, Vasilenko DV (2020) First record of *Leptoomus janzeni* Gibson (Hymenoptera, Chalcidoidea) from Rovno amber. Journal of Hymenoptera Research 80: 137–145. <https://doi.org/10.3897/jhr.80.58882>
- Simutnik SA, Perkovsky EE, Khomych MR, Vasilenko DV (2022a) Two new genera of Encyrtidae (Hymenoptera, Chalcidoidea) with reduced ovipositor sheaths. Journal of Hymenoptera Research 89: 47–60. <https://doi.org/10.3897/jhr.89.79180>
- Simutnik SA, Perkovsky EE, Vasilenko DV (2022b) *Electronoyesella antiqua* Simutnik gen. et sp. n. (Chalcidoidea, Encyrtidae) from Rovno amber. Journal of Hymenoptera Research 94: 105–120. <https://doi.org/10.3897/jhr.94.94773>
- Statz G (1936) Ueber alte und neue fossile Hymenopterenfunde aus den Tertiären Ablagerungen von Rott am Siebengebirge. Decheniana 93: 256–312.
- Statz G (1938) Neue Funde parasitischer Hymenopteren aus dem Tertiär von Rott am Siebengebirge. Decheniana 98A(1): 71–144.

- Telnov D, Perkovsky EE, Kunderata R, Kairišk K, Vasilenko DV, Bukejs A (2022) Revealing Paleogene distribution of the Ptilodactylidae (Insecta: Coleoptera): the first *Ptilodactyla* Illiger, 1807 records from Rovno amber of Ukraine. Historical Biology. <https://doi.org/10.1080/08912963.2022.2136034>
- van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 283: 1–189.
- Yu DS, van Achterberg C, Horstmann K (2016) Taxapad 2016. Ichneumonoidea 2015. Nepean, Ottawa. [database on flash-drive]
- Zaldivar-Riverón A, Belokobylskij SA, León-Regagnon V, Briceño R, Quicke DLJ (2008) Molecular phylogeny and historical biogeography of the cosmopolitan parasitic wasp subfamily Doryctinae (Hymenoptera: Braconidae). Invertebrate Systematic 22: 345–363. <https://doi.org/10.1071/IS07028>
- Zaldivar-Riverón A, Martinez JJ, Belokobylskij SA, Pedraza-Lara C, Shaw SR, Hanson PE, Varela-Hernandez F (2014) Systematic and evolution of gall formation in the plant-associated genera of the wasp subfamily Doryctinae (Hymenoptera: Braconidae). Systematic Entomology 39(4): 633–659. <https://doi.org/10.1111/syen.12078>
- Zherikhin VV (1978) Development and change of Cretaceous and Cenozoic faunistic complexes. Proceedings of the Palaeontological Institute 165: 1–197.
- Zuparko RL, Poinar Jr GO (1997) *Aivalykus dominicanus* (Hymenoptera: Braconidae), a new species from Dominican amber. Proceedings of the Entomological Society of Washington 99(4): 744–747.